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**Wading Hypotheses on the Origin of Human Bipedalism**

At least 30 or so distinct ideas have been published in the scientific literature since the time of Charles Darwin pertaining to the origin of human bipedal locomotion and attempting to explain it in evolutionary terms. Some of them overlap and are complementary, whilst others vary widely and are contradictory. Each of them has strengths and weaknesses but there have been no published attempts at objectively comparing and evaluating them. Their popularity, or otherwise, according to the way they are presented in university texts, appears to be largely a matter of what is currently appealing to authorities of the day.

One idea that has never been popular is the Wading Hypothesis. Here the idea is described in detail, discussed, assessed and objectively compared to other ideas, including those that are *de rigueur* today. Contrary to the mainstream view in anthropology today, it is argued here that there is nothing in the literature that adequately rejects the wading hypothesis, and that it is actually one of the strongest ideas yet proposed, deserving far more serious attention than it has been afforded to date.

A “River Apes ... Coastal People” wading model is introduced. This three-phased model of the evolution of human bipedality proposes a wading-climbing Last Common Ancestor of *Gorilla-Pan-Homo* (LCA-GPH), a seasonally flooded gallery forest habitat for the evolution of hominin bipedality, and a largely coastal foraging phase to optimise our modern efficient, striding gait.

KEY WORDS: *Wading Hypothesis*,  
*human bipedalism*.

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**Hypotheses of Human Bipedal Origins: An Embarrassment of Riches?**

One of the most profound differences between humans and the nearest relatives among the great apes, is their usual mode of locomotion. Chimpanzees, bonobos, gorillas and (but perhaps to a slightly less predictable extent) orangutans, tend to move on all fours when on dry land, like most mammals do. Humans, in remarkable contrast, are obligate but efficient bipeds – few mammalian species have such a limited locomotor repertoire.

How this situation came about has puzzled anthropologists for over 150 years, ever since Darwin enlightened us with the concept of evolution through natural selection, although any review of the specialist literature will show that the field has not been lacking in ideas to solve the problem. So many have been published, in fact, that it prompted Kevin Hunt to ask whether it was an embarrassment of riches, or just an embarrassment? (Hunt, 2001).

Whether it is an embarrassment or not, however, throughout this review it should be remembered that in historical sciences such as palaeoanthropology, it is highly unlikely that the actual evolutionary cause that drove even as remarkable a change as this, will ever be known. All that really can realistically be done is to dispassionately look at the evidence, and the competing hypotheses that have been proposed, and try to determine which ones are the most plausible, most supported by evidence and contradicted by the fewest facts.

### **Classification of Published Bipedalism Models**

There are some 30 or so distinct ideas, published in the literature about human bipedal origins. Many overlap and are complimentary, whilst others are quite distinct and contradictory.

The table below lists and classifies them according to mode of selection (based on Rose, 1991.)

Detailed descriptions and discussions of these models can be found in Kuliukas (2011a) and in the supporting materials on-line.

Rose's (1991) review of published models of bipedal origins was not the first, or the last, although it is unusually comprehensive in the models it lists (see, e.g., Niemitz, 2002; Kingdon, 2003; Stanford, 2003; Jablonski et al., 2004; Harcourt-Smith, 2007; Filler, 2007).

Most university level texts pertaining to human evolution highlight a few of what were considered the most plausible ideas on bipedal origins, at the time, by the author(s). A brief meta-analysis of the way bipedal origins models were reported in such texts in recent years showed that the most popular ideas are carrying models, food procurement and energy efficiency (see Kuliukas, 2011a, for details.) For this reason the pros and cons of these three models are briefly outlined here.

#### ***Carrying Models***

The idea of switching from a four limbed mode of locomotion to one just using the hind limbs has been associated with the concept of "freeing the hands" for decades, ever since the time of Charles Darwin. The carried object or objects proposed to have driven such a remarkable shift in locomotion have varied dramatically, however. Tools, infants, food, gifts, weapons etc., have all been suggested over the years (see Table 1 for citations). Carrying any of these objects seems to convey the notion of selective advantage, and humans do carry lots of things, so the idea feels intuitively right.

The problem is that the concept is a little teleocentric: Just because modern humans carry a lot of things today, and do so bipedally, it does not mean that this is the *reason* why our bipedalism evolved in the first place. Such models do not discriminate between cause and effect. Chimpanzees often carry things adequately whilst knuckle-walking –

TABLE 1 – Bipedal Models Classified By Mode of Selection.

Published Bipedalism Models Classified by Mode of Selection			
Category	Sub-Category	Specific Idea	Original Proponent(s)
Forelimb pre-emption (Carrying)	Unspecified	General freeing of the hands	Darwin 1879; Hooton 1945
		Carrying food back to gallery forest bases.	Hewes 1961
	Food carriage	Carrying and scavenging	Isaac 1978
		Migration-carrying hypotheses	Sinclair et al 1986
		Male Provisioning	Lovejoy 1981;
		Female driven infant carrying	Etkin 1954 ; Tanner (1981)
		Weapon Throwing	Fifer 1987; Dunsworth et al 2003.
Tool carriage	Tool carriage	Bartholomew & Birdsall 1953; Washburn 1960 ; Marzke 1986 ;	
	Weapon wielding	Dart & Craig 1959 ; Kortland 1980	
Social Behaviour	Nuptial gifts	Nuptial gifts	Lovejoy 1981 ; Parker 1987
	Aggression (interspecific)	Inter-specific threat displays.	Kortland 1980
	Threat display (intraspecific)	Intra-specific threat displays	Livingston 1962; Wescott 1967; Tanner 1981; Jablonski & Chaplin 2004
	Evasion/Vigilance	Sentinel behaviour (peering over the savannah)	Reynolds 1931 , Dart 1959 ; Day 1977; Ravey 1978; Walter 2004
	Sexual display	Phallic display directed at females	Tanner 1981
	A new 'fashion'	Copied gimmick idea	Dawkins 2004
Feeding	Terrestrial Gathering	Seed Eating	Jolly 1970
		Terrestrial squat feeding on the forest floor	Kingdon 2002
		Other gathering	Du Brul 1962 ; Wrangham 1980; Rose 1984
	Postural Feeding	Postural feeding hypothesis	Hunt 1994
	Arboreal Predation	Arboreal predation	Eickhoff 1988
	Terrestrial Predation/Scavenging	Stalking	Geist 1978
		Specific Hunting	Cartmill 1974 ; Carrier 1984 ;
		General scavenging/hunting	Szalay 1975 ; Merker 1984; Shipman 1986; Sinclair et al. 1986
	Habitat compulsion	Wading	Coastal foraging
"Aquariboreal" model			Verhaegen et al. 2002
Amphibische Generalistentheorie			Niemitz 2002
Wetland foraging			Ellis 1991; Wrangham et al 2009
Arboreal		'Hylobatian' (Brachiator ancestor) Model	Keith 1923; Prost 1980
		"Upwardly mobile"/vertical climbing hypothesis	Tuttle 1975, 1981
Other		'Orang-utan-like' hand assisted bipedalism	Thorpe et al. 2007
		Variability selection hypothesis	Potts 1998
Efficiency of Locomotion	Slow, long-distance walking	Slow, long-distance walking	Rodman & McHenry 1980; Sockol et al. 2007
		Biomechanical inevitability	Reynolds 1985
	Efficiency of moving from tree to tree.	Efficiency of moving from tree to tree	Pickford & Senut (2001)
	Locomotor "de-coupling."	Locomotor de-coupling	Sylvester 2006
	Exaptation from 'Endurance running'	Endurance running	Lieberman 2007
Selection for better Thermoregulation	Savannah sweat cooling	Thermoregulatory hypothesis	Wheeler 1984
Dietary Factors	Iodine deficiency and/or overly rich Calcium diet	Iodine deficiency	de la Marett 1936
Random Genetic Factors (Mutation/Drift)	Mutation in a key gene involved in vertebral development	"Evo Devo" mutation	Filler 2007
Combination of factors	Combination of factors	Multi-factorial	Napier 1964; Sigmon 1971; Rose 1984 ; Day 1986

either by holding the item in the mouth or by moving tripodally. Indeed, whilst in trees, they are likely to carry things with their feet. The point has therefore been made whether bipedalism has so much freed the hands, rather than enslaving the feet (e.g., Graslund, 2005).

### ***Food Procurement***

The motive of improved food procurement is a rather obvious candidate for selective advantage and many researchers have looked for evidence in this area. Kevin Hunt, for example, studied chimpanzees in Gombe, Tanzania, assuming that behavioural contexts of bipedalism in our nearest relatives might offer clues as to why this became the obligate mode of locomotion in our ancestors (Hunt, 1994, 1996). In over 700 hours of study, he found instances of bipedality to be rare – around 3% of all observed incidents – and that almost all of them were in trees. It should be noted that Hunt’s definition of bipedalism was merely that greater than 50% of the body weight was judged to be on their hind limbs, even if the forelimbs were being used as support. Almost no incidents of unsupported bipedal locomotion on the ground were observed. Hunt’s model, however, is at least based on solid empirical evidence and cannot be accused of the sort of anthropocentric bias associated with carrying models.

The problem with the “postural feeding” hypothesis is in providing convincing scenarios of food procurement that would discriminate favourably for bipedal apes over quadrupedal ones. Hunt proposes that it could have been at the edges of forest, where trees were shorter and more spaced out, that hominins might have benefitted from standing up to reach food in low branches - branches that would have been too weak to support the weight of such creatures.

Other feeding-related ideas have been suggested, using very different evidence and suggesting quite different scenarios. For example, Jolly suggested that baboon seed-eating behaviour on the open plains might help explain our bipedality (Jolly, 1970), and Kingdon suggested haunching on the hindlimbs on forest floors, for nuts and other debris fallen from trees, might have been the key factor (Kingdon, 2003). However, none of the feeding models offer a clear cut difference where humans ancestors would have been at a significant advantage to be able to move bipedally where those of the great apes would not have been.

### ***Energy Efficiency***

Another compelling, evidence-based, model that has become very popular is the one promoting energy efficiency as the key driver of human bipedality. Since the classic, but short, paper of Rodman and McHenry (1980) it has become well known that human bipedalism is remarkably efficient at slow, walking speeds, albeit relatively energetically costly, compared to quadrupedalism, at high speeds (however, for a contrary view, see Halsey & White, 2012).

It is commonly understood that many features of the human post cranial anatomy appear to be adaptations to an efficient, “inverted pendulum” extended limbed gait and careful analysis of the gait using EMG show that muscular activity during walking is remarkable, largely by its absence. Whilst walking on perfectly flat, firm, vegetation free substrates – like pavements, carefully manicured lawns and carpets - we are really just gently falling forwards. There is almost no muscular activity used in propulsion whilst walking on perfectly flat substrates, almost all of it is to arrest momentum of the swing of limbs during the gait and to make sure they are placed in the right spot (see, e.g., Inman et al., 1981).

Although it is extremely likely that energy efficiency was a key driver of the evolution of our current anatomy, it is less certain that it was the cause of the shift to bipedalism in the first place. This teleological problem has become increasingly apparent as the earliest fossils of hominin bipeds have been found ever earlier in time, and evidence has emerged placing them in increasingly densely wooded habitats where it is difficult to envisage scenarios where walking on flat substrates could have been advantageous.

### **Evaluative Framework**

As we have seen, even from this very brief and selective assessment of just three popular models, there is much to be considered when assessing the plausibility of ideas about bipedal origins. Upon first hearing, many of these ideas sound very plausible and attractive, but after further consideration, weaknesses can usually be found. The same is undoubtedly true of all the models proposed in the list reported earlier. Each one has its strengths and weaknesses. Like any idea, each one will have supporters who think them rather brilliant and detractors, who think they are rather silly.

What few commentators seem to have considered, at least going by the evidence of 150 years of literature on the subject, is if there might be some way of objectively assessing them. It is perhaps odd, because for an even longer period of time, academics have relied on well known, tried and trusted, techniques of assessing the written work of others. One need only ponder how many student essays have been marked in the time since Darwin, or how many exams have been passed, how many degrees have been given, and PhDs awarded? For many years, academic institutions assess, compare and evaluate complex ideas that have been written down, as fairly and objectively as possible, through marking rubrics, where a set of marks are allocated to what might be deemed the ‘perfect answer’ to a question and then each attempt that either achieves that optimal answer, or falls short, is given a mark accordingly.

This is what I have tried to devise for this subject: An evaluative framework where each model of bipedality can be assessed, and therefore compared and ranked objectively. The evaluative framework I propose here can be criticised, of course, but it has been developed openly so that others can modify it and use their own framework to as-

sess the models.

The details of the framework and my own assessments using it can be found in Kuliukas (2011a) and in the resources on line but here they will be briefly summarised.

***Evaluative Framework criteria.***

14 criteria were identified on which models of bipedal origins might be assessed, grouped under four main headings.

TABLE 2 – Evaluative Framework

<b>“Darwinian”</b>	<b>“Ecological”</b>	<b>“Palaeontological”</b>	<b>“Epistemological”</b>
<b><i>Increases Survival</i></b>	<b><i>Offers Improved Food Acquisition</i></b>	<b><i>Fits known Palaeo-Ecological Record</i></b>	<b><i>Has Extended Explanatory Power</i></b>
<b><i>Favours Reproductive Success</i></b>	<b><i>Decreases Predation Vulnerability</i></b>	<b><i>Explains Anatomical Traits of Early Hominids</i></b>	<b><i>Is Complementary with other Models</i></b>
<b><i>Is not Teleological</i></b>	<b><i>Explains why great Apes are not Bipedal</i></b>	<b><i>Provides Plausible Precursor to both Human Bipedalism and Knuckle-Walking</i></b>	<b><i>Is Falsifiable, or at Least Testable</i></b>
	<b><i>Fits with Examples of Behaviour Visible in Extant Apes</i></b>		
	<b><i>Applies to Both Sexes</i></b>		

In a nutshell, by these criteria, the best models of hominin bipedal origins should increase fitness (or at least not reduce it) of contemporary populations throughout their evolutionary history. They would improve food acquisition, accounting for any increased risk of predation. Ideally, they would not favour one sex over the other. They would be consistent with the known fossil record and offer to explain anatomical anomalies between the earliest bipedal hominins and modern humans. They should also be illustrated by clear behavioural contexts in extant apes. The ideal model should not only explain why humans became obligate terrestrial bipeds, but also why the other extant African great apes did not. Optimally, they should also offer more explanations for other human traits in addition to our bipedality, and be complimentary to other previously published ideas as much as possible. They should be scientifically constructed and offer falsifiable predictions as tests.

### ***Weightings and Assessments***

The evaluative framework has an interactive web page resource to record and calculate overall assessments based on these weightings (see [www.tinyurl.com/BipedalModels](http://www.tinyurl.com/BipedalModels)). It has been put on the web in this way so that others can freely critique the framework and change the weightings according to their own views and enter their own assessments. My own evaluations can be read in detail and compared with any other's.

Suffice it to report here that, by these criteria, I found that wading models were as good as, if not better, than other published models and far better than their relative unpopularity in university texts would suggest.

Most of the rest of this paper will now focus on variations of the wading hypothesis of bipedal origins, and their rather unfortunate history. It will contrast them with the latest fashionable ideas that appear to be in the mainstream today. Finally, I will introduce a variant of the wading model ("River Apes... Coastal People" model), which has been constructed specifically to achieve the highest possible evaluation from this framework.

## **A Brief History of the Wading Hypothesis**

### ***Hardy's Coastal Wading Idea***

The earliest discussion of wading in shallow water in the context of the evolution of human bipedality in the literature is probably most accurately attributed to Alister Hardy (1960) in a short article in *New Scientist* "Was Man More Aquatic in the Past?"

The article was written in response to negative criticism, by some elements of the British press, to a talk he gave a few weeks earlier to the Brighton Sub-Aqua Club. In his talk he outlined his idea, kept to himself for over 30 years, that perhaps man had a more aquatic past. The original impetus to that idea had been man's peculiar (among mammals) layer of subcutaneous fat, but in his *New Scientist* article, he suggested that a "more aquatic" phase might help to explain a whole range of unusual human traits, including our bipedality.

### ***Morgan's "Aquatic Ape Hypothesis"***

Remarkably, there was almost no response to Hardy's "more aquatic" notion apart from a few letters (most of which were positive) in the pages of *New Scientist* over the next few weeks. The one academic paper, published two years later (that was also very positive about the idea) by the geographer, Carl Sauer, specifically considered riparian niches, in addition to Hardy's coastal ones, for early hominids but hardly alluded to the wading hypothesis (Sauer, 1962). Desmond Morris' popular science book "The Naked Ape" also referred to Hardy's "Aquatic Ape Hypothesis" (probably the first to do so by coining that label) positively in 1967 but again, it barely mentioned the bipedalism aspect of it other than to state: "It explains our streamlined bodies and even our vertical posture, the latter supposedly have developed as we waded into deeper and deeper

water” (Morris 1967:29). Other mentions in the decade after 1960 were very rare indeed.

The idea appeared to be heading for complete obscurity when it was seized upon by a successful Welsh television playwright, Elaine Morgan, who stumbled across Desmond Morris’ reference to it in “The Naked Ape”. Her deliberately provocative and controversial book “The Descent of Woman” (Morgan, 1972), published 100 years after Darwin’s “Descent of Man”, had two main themes. The first was to try to critique what she perceived as a very imbalanced, largely male dominated, view of the evolution of mankind. It mocked the well-established, savannah-based “Man the Mighty Hunter” view of our evolution, and it offered a radically different idea in its place. The second aim of the book was to promote that idea: Hardy’s “aquatic ape” hypothesis. The idea that wading might help to explain our bipedality was only briefly mentioned in that first book but her later volumes increasingly focused on it. “The Aquatic Ape” (Morgan, 1982) included one full chapter on the subject. “The Scars of Evolution” (Morgan, 1990), had two and of the 14 chapters of “The Aquatic Ape Hypothesis” (Morgan, 1997) four were specifically about the wading hypothesis of human bipedal origins.

Morgan thus greatly expanded upon Hardy’s original wading idea and explained its main advantage in clear and obviously stark terms: being bipedal in shallow water would provide a clear survival benefit to any early hominin that did so... it would be able to breathe easily whilst in water. Morgan’s books, although praised for being “superbly written” (Tobias, 1998), did not offer any new empirical data and were not written as scientifically as some seemed to expect. However, by 2008 Morgan had put together a rather plausible, carefully argued, model that suggested hominin bipedal origins were due to, at least in part, some wading activity and evidence appeared to be growing in its favour.

When Morgan wrote her first specific chapter on the wading hypothesis (1982) there was little behavioural evidence from extant apes or the fossil record to back her up and few anthropologists took the idea very seriously. Apart from a few isolated reported incidents of bipedal wading in proboscis monkeys, the popular view was that our ape cousins avoided all contact with water. This view has largely changed today, as evidence has emerged showing that great apes sometimes do move in shallow water. Doran & McNeilage (1998) observed slash displays in gorillas, where they were often bipedal. Chimpanzees at Conkuati were observed regularly wading out to boats bipedally and Myers Thompson (2002) reported 24% bipedality in wild bonobos at Lukuru mostly in the context of aquatic foraging.

Very few other Mammalian taxa switch to a bipedal posture in shallow water. Some species of bear, occasionally stand bipedally in water, e.g., whilst looking for salmon, but they will almost certainly return to all fours again when they start to move.

It was also the case that the fossil record was not particularly supportive of a wading origin for human bipedalism when Morgan first promoted her ideas but this has also gradually changed in the years that have followed. Although the evidence that has come out since 1980 has not supported Hardy’s original (coastal), pre-Homo, scenario,

one that Morgan certainly backed, earlier and earlier evidence has emerged for hominin bipedalism, in increasingly wet and wooded, as opposed to dry, open savannah habitats. Although not coastal, these wetland or riparian habitats are certainly consistent with a wading component for early bipedal hominids (see, e.g., Brunet, 2002; Verhaegen et al., 2002, 2011; Wynn et al., 2006).

### *Mainstream Support of Wading Ideas in Bipedal Origins Models*

A few anthropologists have supported the wading idea to some extent. Carsten Niemitz and Richard Wrangham published material supportive of the idea that wading may have been a component in the origin of early hominin bipedal origins, although the idea was not attributed to Hardy or Morgan. Others however, such as Colin Groves and Phillip Tobias, have been more generous in giving credit to the original proponents of this idea.

Carsten Niemitz has promoted wading as a component in hominin bipedal origins perhaps more seriously than any other anthropologist for several years. A series of papers, articles and books promote his “Generalist Amphibian Hypothesis” or “Amphibische Generalisttheorie” (Niemitz, 2002).

Wrangham et al. (2009) published a paper promoting the use of wetland refugia, analogous to the modern day Okavango Delta, as key habitats in early human evolution, and even suggested that the act of moving bipedally through shallow water may have “promoted adaptations for habitual bipedality” in early hominins. They noted that underground storage organs (USOs) have been proposed as critical fall-back foods for early hominins in savannah habitats, and suggested that aquatic habitats could have been a useful source for hominins as shallow aquatic habitats tend to offer high plant growth rates, high USO densities, and relatively continuous USO availability throughout the year. Their study differed from “traditional savannah chimpanzee models” of hominin origins in this key aspect of proposing that access to aquatic habitats was a necessary condition for survival in broader savannah-based macro-habitat contexts (Wrangham et al., 2009) but, again, did not cite Hardy or Morgan.

### *Other Supportive Evidence*

Since 2002 some further evidence in support of the wading hypothesis has been published. In 2002 a pilot study of captive bonobos reported 2-3% bipedality in terrestrial or arboreal contexts but approximately 90% in shallow water wading contexts (Kuliukas, 2002).

The energetic cost of wading in different depths of water, at different speeds, and with different degrees of hip and knee flexion, was compared with the cost of walking on land and it was found that in waist deep water, at 0.6 m/s, the cost of a bent hip, bent knee (BHBK) gait was reduced from 55% on land, to approximately 18% in water. In some depths/knee flexions and speeds, the cost differential was eliminated completely. (Kuliukas et al., 2009) This evidence suggests that wading provides a potentially ideal scenario for early, non-optimal, bipedalism to have evolved.

### ***Historical Summary***

Since Hardy and Morgan first articulated the wading idea, the body of evidence that is consistent with it has grown and as no significant findings have been reported in that time to contradict it, it begs the question: What has the mainstream response to the wading hypothesis been? According to the evaluative framework used here, the various wading hypotheses appear relatively strong, yet it would appear they are rarely promoted to students of palaeoanthropology as potential research topics. Indeed most students seem to be given the impression that they have simply been rejected. The question, then, needs to be addressed: If they have been rejected, which papers should be cited that make that refutation and on what basis did they do so?

### **The Rejection of the Wading Hypothesis?**

Considering how simple, plausible and evidence-based the various wading hypotheses are, it is remarkable how little scientific attention they have received. Anyone looking for the definitive paper in the scientific literature that represents the rejection of the idea will have a frustrating time.

What follows is a fairly comprehensive review of the (rather tiny) literature critiquing the wading idea up until 2013.

The most specific critical consideration of the wading hypothesis in the literature is still to be found in Roede et al. (1991). This volume is the proceedings of a symposium on the “Aquatic Ape Hypothesis” held in Valkenburg, Holland, where proponents and skeptics of the “aquatic ape” idea, in general, met to discuss it. Two papers in the symposium considered, and rejected, the idea that wading in shallow water was likely to have been a factor in the evolution of human bipedalism.

The first, by Ghesquiere & Bunkens (1991), investigated the energy efficiency of wading “up to the arm pits” of subjects and rejected the idea on the basis that it was four times more costly to do so than on land at 0.4m/s. The possibility that the difference in cost might have been less in shallower water, or at slower speeds, was not considered.

The other paper was by Preuschoft & Preuschoft (1991). They discussed the epistemology of proponents of the so-called “Aquatic Ape Hypothesis” and, quite fairly, criticised them for not making falsifiable predictions and setting about testing them. In that context they set out to test two different “aquatic” hypotheses – one fairly extreme and one relatively mild. The mild one was more or less the wading hypothesis. They claimed to test it by comparing anatomical features of animals known to wade bipedally – wading birds - with human beings, and rejected the idea on the basis that wading birds tend to have very long tibiae, compared to humans. It was not considered that, unlike wading birds, early hominin bipeds were almost certainly also climbing trees and that this would have posed considerable counter pressure to elongating the tibiae.

These two papers in Roede et al. (1991) are still, as far as I can gather, the only ones to specifically consider some kind of wading hypothesis in scientific terms and even then, the Preuschoft & Preuschoft paper considered it alongside a more extreme “full on” aquatic hypothesis.

The most cited, and respected, critique of the “Aquatic Ape Hypothesis”, in general, is that written by John Langdon (1997). In it, he lined up 26 human traits that Elaine Morgan had claimed were evidence of a more aquatic past and basically argued that each had better alternative (non-aquatic) explanations. His main argument in the paper was that any claim of parsimony that proponents of these ideas might have – that such an odd cluster of peculiar traits that make us different from chimps might all be explained by one, relatively simple and relatively modest switch in habitat to one involving more wading, swimming and diving – is flawed.

His method in rejecting each of these traits was perfunctory, however, to say the least. His rejection of the wading idea is illustrative of his approach and is described here in full. Langdon (1997) only considered one argument, of many, in favor of wading from its main proponent: Morgan (1981) suggested that peculiar human conditions such as hernias and varicose veins, which appear to have resulted from a switch to bipedalism, may have been less problematic, and hence more understandable, if this bipedalism had first been practiced in the context of wading. Langdon did not challenge that assertion, even by stating the obvious retort that such uniquely human conditions may be simply due to extended ageing. Instead he complained that “authors who wish to recite the many disadvantages of bipedalism commonly do so by comparing humans to medium-sized terrestrial quadrupedal mammals” Langdon (1997:481). His argument included no criticisms of the wading idea itself, but instead advocated vertical climber/brachiationist models, which are, in any case, quite compatible with some wading models (e.g., Verhaegen et al., 2002). In a table listing traits which have been argued to support the so-called “Aquatic Ape Hypothesis” (AAH), Langdon simply noted: “Bipedalism - not typical of aquatic animals” Langdon (1997:488). This superficial treatment does no justice to Morgan’s work, which includes eight chapters on bipedal origins in five books, a treatment which two Australian anthropologists recently noted has “reached a sophistication that simply demands to be taken seriously” (Groves & Cameron, 2004:68). See Kuliukas (2011b) for a full critique of Langdon’s refutation of the “AAH’s” parsimony.

This is not a comprehensive review of rebuttals of the wading hypothesis in the literature, but I believe it includes the most significant ones. Other papers that included some reference to the idea were dismissive and either suggested personal favourites from the list above or else ignored the matter completely.

The only objective conclusion a student of this subject should make, upon a review of the literature, is that if the wading hypothesis has been rejected at all, it has been done so on the flimsiest of grounds on the basis of almost no serious scientific investigation.

### What is the Contemporary Mainstream View?

So if mainstream anthropologists today are dismissive of the wading arguments, what do they offer instead? What actually is the “mainstream” view today?

It might be argued by some that most of the 30 or so models listed earlier are outdated and that a growing consensus is forming among some experts in the field about this question. Certainly, some of the long held assumptions about how the last common ancestor (LCA) of hominins and chimpanzees moved are currently being challenged, but it is not clear from the literature how these new approaches fundamentally change any of the big issues. Indeed more new questions appear to be being posed than are being answered.

Basically, the most popular assumption held, by most workers in the field, for most of the last 150 years, would appear to be that the LCA was more chimp-like than human-like in the way it moved. Even when it was not envisioned that the LCA was actually a quadrupedal knuckle-walker, in the way extant chimpanzees and gorillas are today, it was certainly widely held that that when the LCA moved bipedally it must have done so in a relatively inefficient, chimp-like way, with a bent-hip-bent-knee (BHBK) gait – and certainly not like we do.

This posed a few key questions: In what scenarios would a relatively inefficient gait such as this be plausible? And: Assuming modern human bipedal efficiency came *as a result of* anatomical changes, adaptations for the need for more efficient bipedalism, what scenarios might help induce this “energetic rubicon” of efficiency to be crossed?

One prominent dissenting voice to that view has long been Owen C. Lovejoy. Apparently, upon seeing the very first australopithecine fossil specimen from Hadar, found by Johanson et al. – a proximal tibia, Lovejoy decided that this species must not only have been bipedal, but that it walked with a fully extended limb, as we do.

In the late 1990s there were a number of entertaining exchanges of opinion between those, like Latimer, who agreed with Lovejoy and those who didn't, like Berge, Stern and Susman (see, e.g., Berge, 1994; Stern, 2000). In more recent years, however, literature supporting a BHBK-based assumption about early hominins has been conspicuous by its absence, and the view that early hominins walked like we do has become dominant.

Over the last 15 years, or so, evidence has accumulated indicating that LCA of all the great apes may have already been somewhat upright and interpretation of evidence pertaining to the evolution of the spine has been confidently interpreted by several leading authorities in the field, such as Lovejoy and collaborators, that early hominins, such as australopithecines, may have adopted a remarkably human-like gait with fully extended limbs.

Aaron Filler's book “The Upright Ape – A New Origin of Species” (Filler, 2007) gave the idea that bipedalism had preceded the last common ancestor of humans and great apes credibility and impetus. His argument that rapid evolution (through saltatory developmental mutations) of the hominin vertebral column could have been a key factor

in the adoption of upright posture fitted neatly into the increasingly fashionable “Evo Devo” approach to evolution.

In the years that followed, McCollum et al. (2010) published data supporting the early evolution of more human like axial skeletons in ape ancestors. This, it was argued, indicated that the LCA of humans and great apes, rather than being ape-like in form, was more likely to be human-like, having sufficient lumbar vertebrae and flexibility to support lordosis and, by implication, a fully upright posture.

The long awaited publication of the findings of *Ardipithecus ramidus* (see, e.g., Lovejoy et al., 2009) also supported the new emerging paradigm as the fossil evidence again indicated an earlier bipedality than was previously held.

Meanwhile other papers consolidated similar views using other evidence. Carey & Crompton (2005) published a study of human subjects walking 55% more inefficiently with a BHBK gait on treadmills, than with a fully upright posture. They used it to support their contention that Australopithecines could not have walked with a BHBK gait. This was supported by other studies, of computer simulations (e.g., Sellars et al., 2005).

Furthermore, Sockol et al. (2007) published a study of extant chimps questioning the most fundamental assumptions about the inefficiency of a chimp-like (i.e., BHBK) gait. They reported significant variation in the energy efficiency of locomotion in a small chimp population. Simply walking with more extended limbs made a few of them sufficiently efficient with an upright gait to question if early non-optimal hominoids had any energetic rubicon to cross for after all.

All of this, without any significant contrary reply, seems to signal the demise of the view that early hominins may have walked with a BHBK gait and, indeed, Lovejoy et al. recently published a paper confidently explaining “why no hominids ever relied on a bent-hip -bent-knee gait” (Lovejoy & McCollum, 2011). Their argument relies on the assumption that the chimp-like BHBK gait is due to their inflexible lumbar vertebrae (specifically an inability to exhibit lordosis) and that the LCA of humans and great apes did not possess this inflexibility. Whether this assumption is strictly correct or not, the idea that even early bipedal hominins such as *Australopithecus afarensis*, let alone the LCA of all great apes, already had postcranial traits “with highly advanced adaptations to a striding, bipedal gait” (Lovejoy & McCollum, 2011:3299) only poses more questions.

If Lovejoy is right that gracile australopithecines walked with a fully extended human-like gait, why is their post cranial anatomy so different to ours? How and why did they do so in habitats that were probably far from ideal for efficient, striding bipedalism? If australopithecines were already walking optimally, how did this behaviour begin? What preceded it? Were the traits that make them efficient terrestrial bipeds a fortuitous exaptation for something else that came earlier? If so, what? Was the LCA of the ape lineage already a brachiator, like modern *Hylobates*? Or is that a specialist, more recently derived, mode of locomotion? Perhaps most importantly – If the LCA was already bipedal, why did one lineage continue to move with a striding gait, but the ancestors of *Pan* and *Gorilla* stop doing so, switching instead to a peculiar knuckle-waling form of quadrupedalism?

Lovejoy and McCollum (2011) do discuss these issues to a degree. The LCA is proposed to have practiced “a pattern of cautious climbing that combined above-branch palmigrady with occasional below branch suspension, enhanced by a highly mobile, lateralized shoulder girdle in combination with marked wrist adduction and elbow extension” (Lovejoy & McCollum, 2011:3291) but it is not clear how this might act as a preadaptation to the fully extended kind of bipedal locomotion that they argue must have followed.

As they put it “The most salient question remaining, of course, is the issue of the eventual adoption of bipedality in hominids. Why did hominids exchange palmigrade/plantigrade quadrupedality for upright walking?” Their answer to that continues to be to promote Lovejoy’s long running theory on the matter: “The most likely explanation for the adoption of terrestrial bipedality, in our view, continues to involve novel adaptations in hominid social structure that required upright locomotion for carrying” (Lovejoy & McCollum, 2011: 3292), Lovejoy’s Provisioning Hypothesis (Lovejoy, 1981).

It is difficult to know if Lovejoy’s views are supported by even a majority of paleo-anthropologists today and there are other ideas still being actively promoted. Thorpe et al. (2007) made the front page of *Science* with their “thin branch orang-utan-like upright locomotion” ideas and the endurance running hypotheses about human bipedal origins have also regained popularity recently (see, e.g., Lieberman et al. 2006; Lieberman, 2007, 2012).

It’s a situation that has long been criticised. Rose (1991:38) admitted that “despite a voluminous literature, our ignorance concerning bipedalization is almost complete”. Hunt (2001) described the literature of ideas on the subject as a “tangled thicket” and the special edition of the *Journal of Anatomy* on the subject included a key paper which concluded by asking “whether the evolution of bipedalism was a more complex affair than has previously been suggested.” (Harcourt-Smith & Aiello, 2004:413). It is suggested here that, almost a decade later, the current mainstream view on human bipedal origins, whatever it is, still lacks any real clarity on the key questions outlined above.

Meanwhile, over fifty years after their first publication, the wading hypotheses have clearly not yet even been properly considered, let alone rejected. It would appear that discounting the wading hypothesis without the need for any scientific rigour is the one thing most anthropologists are happy to agree on.

### **River Apes... Coastal People Model**

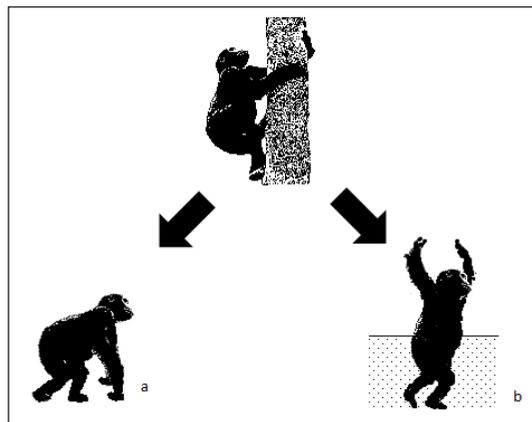
This review paper will end by outlining a three-stage model for human bipedal origins which, I argue, satisfies the evaluative framework discussed earlier and potentially answers many of the key questions that the mainstream view does not.

***Phase 1 – Wading-Climbing LCA (Miocene 15Ma – 5.2Ma)***

Along with the growing consensus, this model assumes that the LCA of Gorilla/*Pan/Homo* (LCA-GPH) was already *somewhat* bipedal but not efficient obligate bipeds like we are. The increasing fossil evidence of early hominids with anatomical traits consistent with upright posture, at the very least, backs this assumption.

It is noted here that despite some authors' confidence about how the LCA moved (e.g., Lovejoy & McCollum, 2011) there is still actually no generally agreed consensus fossil candidate for the paleospecies and therefore no good evidential basis for any proposed locomotor repertoire they might have used. Contrary to most authorities, but in agreement with some (e.g., Harrison, 1991), it is suggested that *Oreopithecus bambolii* is as good a currently known candidate in the fossil record as any other. There is contradictory evidence about this paleospecies, some indicating that *Oreopithecus bambolii* was somewhat bipedal (e.g., Harrison, 1991; Rook et al., 1999; Kohler et al., 2003) whilst others take an opposing view (e.g., Susman, 2005; Lovejoy & McCullom, 2011).

It is suggested that positing a locomotor repertoire comprising significant amounts of wading and climbing may well solve this paradox. The paleological evidence suggests that *Oreopithecus bambolii* lived in a swampy island niche consistent with a locomotor repertoire consisting of significant wading and climbing. It is these two substrates together that, it is suggested, provide an ideal scenario for early hominid upright posture and the earliest forms of bipedalism. Evidence from extant apes clearly indicates that shallow water compels bipedal locomotion (not just posture) like no other substrate. Whereas extant vertical climbing apes tend to switch quadrupedal locomotion when they climb down onto dry land, in swampy habitats they stay upright in the shallows. This shows that vertical climbing alone is an insufficient precondition for early bipedalism. The terrestrial "bipedalism" of *Hylobates* or *Ateles* can be seen as a highly derived condition from very specialised brachiation.



*Figure 1. Wading-Climbing Early Bipedalism.*

Vertically climbing extant apes switch to quadrupedal knuckle-walking on dry ground (a), but continue to move in an upright posture when in shallow water (b).

To test if this phase of the model is correct, some simple predictions can be made:

1. The earliest fossil evidence for hominid bipedalism should be associated with swampy/wooded habitats.
2. Earlier candidates for the LCA of Pongo and African Great Apes should be found in Mediterranean/Tethys coastal habitats, again indicative of swampy habitats.
3. The LCA of African Great Apes and *Homo* should be found migrating south from the Mediterranean/Tethys, perhaps closely associated with Sahelanthropus and its Lake Chad habitat.

***Phase 2 – Terrestrial Bipedalism Evolving in Seasonally Flooded Gallery Forest Refugia in Australopithecine-Grade Hominins, Knuckle-walking in other African Apes (Pliocene, 5.2Ma – 2.6Ma)***

Consistent with the “savannah-based paradigm” held by most anthropologists for most of the last hundred years, and specifically Coppens’ (1994) “East-Side Story”, the second phase proposes that rifting in East Africa was the major factor in the *Pan*-Gorilla/*Homo* split. West of the rift valley, ancestors of chimpanzees and gorillas became adapted to tropical rainforest habitats resulting in more climbing and less wading. Moving through dense vegetation in uneven substrates favoured a reversion to more quadrupedal locomotion and knuckle-walking specifically, as a formerly somewhat-bipedal ape increasingly looked to move on all fours and support its weight with extended forelimbs.

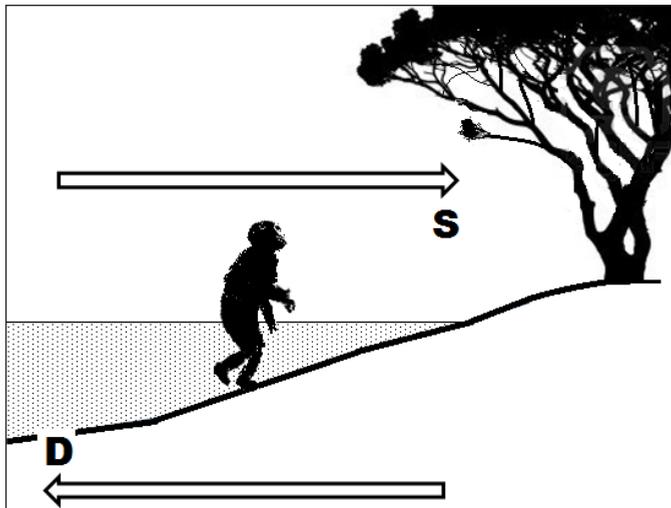


Figure 2. Shallow water provides a continuum of depths – ideal for the early adoption of terrestrial bipedalism.

East of the rift, it is suggested that the lineage represented by australopithecine grade hominins were exposed to a shift to a much more arid environment. Savannahs, however, are still characterised by seasonal rainfall and although, generally speaking, forests were replaced by open plains, tree density would not have been reduced evenly. Gallery forests would have provided suitable refugia for hominins that had evolved in wet and wooded habitats for millions of years. Seasonally flooded for several weeks, perhaps twice a year, such habitats provide an ideal scenario to simultaneously (in evolutionary terms) guarantee more bipedalism (in waist deep water, hominins have little choice) and also encourage greater efficiency for terrestrial bipedalism.

In Shallow Water (S), there is less hydrostatic support for upright posture, less compulsion to move bipedally, but greater selection for anatomical traits to make terrestrial bipedalism efficient.

In Deep Water (D), there is more hydrostatic support and more compulsion to move bipedally, but less selection for traits to make bipedalism efficient.

The Pliocene was characterised not only by a shift towards greater aridity, but also to greater shifts in seasonality both in phase frequency and amplitude (Potts, 1998) and many hominin fossils have been associated with riparian habitats (see, e.g., Wynn et al., 2006). Kingdon’s (2003) whole evidence-based thesis for bipedal origins is based on gallery forest habitats flowing east into the Indian Ocean. The key difference here is that it is proposed that wading through the riverine borders on the inside of such habitats was the major driver for greater bipedalism, rather than the dry forest-floors on the outside borders where, Kingdon argues, ground-dwelling hominins’ haunching would give them anatomical exaptations for bipedalism.

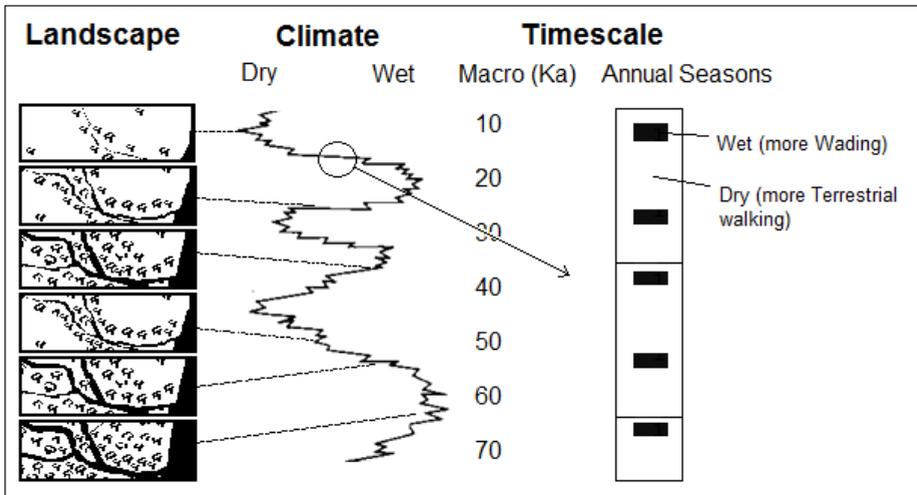


Figure 3. Seasonally flooded gallery forests favour both wading and Terrestrial Bipedalism (Adapted from Potts 1998)

As climate varies on a macro scale (over thousands of years) tree cover recedes closer to permanent water courses during periods of aridity, or spreads out generally during wet periods. These broad macro-changes are superimposed upon regular annual seasons with one or two wet seasons per year, where local gallery forest habitats would become flooded or have exposed, dried out river beds.

This phase predicts that:

1. Anatomical differences (such as the shape of the australopithecine pelvis, relatively large feet) between Pliocene hominins and modern humans may be explicable as adaptations to more wading.
2. Gallery forest and other wetland habitats will continue to be associated with australopithecine-grade hominins.

### ***Phase 3 – Efficient Coastal Foraging in Homo (2.6Ma – 200Ka)***

The final phase of the model attempts to explain the undoubted anatomical adaptations for efficient terrestrial bipedalism that distinguish modern humans from our great ape cousins in a waterside context. As rivers lead to the sea, it is proposed that it would only be a matter of time before populations of hominins inhabiting seasonally flooded gallery forest refugia, in a broad savannah context, would find themselves by the large rift valley lakes or by the Indian ocean coast, where the effects of aridity and seasonality on food supplies would be less severe.

Again, consistent with many models, it assumes that these provided a selective advantage to early humans for slow, long distance locomotion. However, it notes that this efficiency is optimal on the kind of specific substrates that modern humans tend to create for themselves – those that are perfectly flat, firm and vegetation-free. It proposes that for human anatomy to have evolved optimally for such habitats it is logical that they moved through substrates analogous to them for much of the time.

In the natural world, substrates that are ideal for walking (i.e., flat, firm and vegetation-free, analogous to the man-made carpets and pavements which came along much later) include waterside habitats. Dried out river beds, coastal flats and beaches, right by the water's edge are almost uniquely flat and firm enough to allow the kind of fully extended striding gait that allows for our bipedal efficiency. Following behind massive herds of savannah ungulates might also qualify, perhaps, but it is argued that even savannah grasslands often have significant vegetation which would hinder efficient bipedalism and, of course, there is the small matter of the risk of predation.

The topology of coastal habitats, such as river deltas coastal lagoons and spits by their very nature, are likely to be convoluted and oddly shaped, requiring longer distances to be covered, per km<sup>2</sup>, than in-land niches. Furthermore the ecology of coastal habitats makes them less vulnerable to predation, compared to open savannah and other in-land habitats, making slow, efficient, locomotion a more plausible adaptive benefit. In a nutshell, it proposes that the earliest members of the genus *Homo*, and later, *Homo sapiens*, were coastal foragers.



Figure 4 – Ideal place for long distance walking

This phase makes several predictions:

1. Evidence of the very earliest modern humans should be found in or near coastal habitats (see, e.g., Marean et al., 2007, for some evidence of this.)
2. The most optimal naturally occurring substrates to walk efficiently are waterside habitats such as dried out river beds and flat, wet sandy beaches.
3. The earliest *Homo erectus*/ergaster grade hominins should also be found in coastal habitats.

### Summary

Wading hypotheses offer a regime of selective advantage that is simpler and more clear-cut than any other. They are among the least teleological in that extant ape behaviour is perhaps their best supporting evidence. They offer improved food acquisition, especially in the context of aridification in broad savannah contexts with the use of fall-back foods in wetlands or simply in inhabiting gallery forest refugia. They are consistent with the known fossil record and offer explanations of other anomalous traits of the earliest hominin bipeds. They provide a more plausible and elegant precursor to both human bipedalism and *Pan*/Gorilla knuckle-walking than other models. Epistemologically, they complement most other models and have extended explanatory power if one assumes waterside models of later human evolution.

Their unfortunate association with the so-called (probably mislabelled) “Aquatic Ape Hypothesis” has led to them being unfairly dismissed, but any objective review of the literature will find this “rejection” severely lacking.

The current mainstream view on human bipedal origins is as confusing today as it has been for decades. It is long overdue that more of the various falsifiable predictions made by wading hypotheses are taken seriously and tested scientifically.

## References

For on-line resources see - [www.tinyurl.com/BipedalModels](http://www.tinyurl.com/BipedalModels) or [www.waterside-hypotheses.com](http://www.waterside-hypotheses.com)

- Bartholemew, G.A., & Birdsell, J.B. (1953). Ecology and the Protohominids. *American Anthropologist*, 55: 481-498.
- Berge, C. (1994). How Did the Australopithecines Walk? A biomechanical Study of the Hip and Thigh of *Australopithecus afarensis*. *Journal of Human Evolution* 26: 259-273.
- Brunet, M. (2002). *Sahelanthropus tchadensis* (Late Miocene of Chad), the Earliest Hominid. *Nature*, 418: 145-151.
- Cameron, D.W., & Groves, C.P. (2004). *Bones, Stones and Molecules ("Out of Africa" and Human Origins)*. Sydney: Elsevier.
- Carey, T.S., & Crompton, R.H. (2005). The Metabolic Costs of 'Bent-Hip, Bent-Knee' Walking in Humans. *Journal of Human Evolution*, 48(1): 25-44.
- Carrier, D.R. (1984). The Energetic Paradox of Human Running and Hominid Evolution. *Current Anthropology*, 25: 483-494.
- Cartmill, M.(1974). Rethinking Primate Origins. *Science*, 184: 436-443.
- Coppens, Y. (1994). East Side Story. *Scientific American*, May: 62-69.
- Dart, R.A., & Craig, D.(1959). *Adventures with the Missing Link*. Philadelphia: The Institution Press.
- Darwin, C. (1879). *The Descent of Man and Selection in Relation to Sex. 2 Vols*. London: Murray.
- Dawkins, R.(2004). *The Ancestor's Tales*. London: Weidenfeld and Nicolson.
- Day, M.H. (1986). Bipedalism and Prehistoric Footprints, In Wood B., Andrews P., Martin L. (Eds) *Major Topics in Primate and Human Evolution*. New York: Cambridge University Press.
- Day, M.H. (1977). Locomotor Adaptation in Man. *Biology and Human Affairs*, 42: 149-151.
- de la Marett, J.R. (1936). *Race, Sex and Environment*. London: Hutchinsons Scientific.
- Doran, D.M., & McNeilage, A.(1998). Gorilla Ecology and Behaviour. *Evolutionary Anthropology*, 6(4): 120-131.
- Du Brul, E.L. (1962). The General Phenomenon of Bipedalism. *American Zoologist*, 2: 205-208.
- Eickhoff, R.(1988). Origin of Bipedalism - When, Why, How and Where? *South African Journal of Science*, 84: 486-488.
- Ellis, D.V. (1991). Is an Aquatic Ape Viable in Terms of Marine Ecology and Primate Behaviour? In Reynolds V., Roede M., Wind J., Patrick J. (Eds) *Aquatic Ape: Fact of Fiction: Proceedings from the Valkenburg Conference*. London: Souvenir Press.
- Etkin, W. (1954). Social Behaviour and the Evolution of Man's Mental Faculties. *American Naturalist*, 88: 129-142.
- Fifer, F.C. (1987). The Adoption of Bipedalism by the Hominids: A New Hypothesis. *Human Evolution*, 2: 135-147.
- Filler, A.G. (2007). *The Upright Ape - A New Origin of the Species*. Franklin Lakes: New Page.
- Geist, V. (1978). *Life Strategies, Human Evolution, Environmental Design. (Towards a Biological Theory of Health)*. New York: Springer-Verlag.
- Ghesquiere, J., & Bunkens, H. (1991). The Burden of Locomotion in Water: Could the Aquatic Ape Have Overcome It? In: Reynolds, V., Roede, M., Wind, J., Patrick, J. (Eds) *Aquatic Ape: Fact of Fiction: Proceedings from the Valkenburg Conference*. London: Souvenir Press.

- Graslund, B. (2005). *Early Humans and their World*. London: Routledge.
- Halsey, L.G., & White, C. R. (2012). Comparative Energetics of Mammalian Locomotion: Humans Are Not Different. *Journal of Human Ergology*, 63: 718-722.
- Harcourt-Smith, W.E.H., & Aiello L.C. (2004). Fossils, Feet and the Evolution of Human Bipedal Locomotion. *Journal of Anatomy*, 204(5): 403-417.
- Harcourt-Smith, W.E.H. (2007). *The Origins of Bipedal Locomotion*. Berlin: Springer-Verlag.
- Hardy, A. (1960). Was Man More Aquatic in the Past? *New Scientist*, 7: 642-645.
- Harrison, T. (1991). The Implications of *Oreopithecus bambolii* for the Origins of Bipedalism. In Cop-pens Y.Senut B. (Eds) *Origine(s) de la bipédie chez les hominides*. Paris: CNRS.
- Hewes, G.W. (1961). Food Transport and the Origin of Hominid Bipedalism. *American Anthropologist*, 63: 687-710.
- Hooton, E.A. (1945). "Young Man, You Are Normal" Findings From a Study of Students. New York: GM Putnam's & Sons.
- Hunt, K.D. (1994). The Evolution of Human Bipedality: Ecology and Functional Morphology. *Journal of Human Evolution*, 26: 183-202.
- Hunt, K.D. (1996). The Postural Feeding Hypothesis: An Ecological Model for the Evolution of Bipedalism. *South African Journal of Science*, 92: 77-90.
- Hunt, K.D. (2001). *The Tangled Thicket of Bipedalism Origin Hypotheses: Embarrassment of Riches or Just Embarrassment?*. Am. Assoc. Anthropol. Meeting, Washington, D.C.
- Inman, V.T., Todd, F.N., & Ralston, H.J. (1981). *Human Walking*. Williams & Wilkins. Philadelphia.
- Isaac, G.I. (1978). The Archaeological Evidence for the Activities of Early African Hominids. In Jolly C. J. (Ed) *Early Hominids of Africa*. London: Duckworth.
- Jablonski, N.G., & Chaplin, G. (2004). Becoming Bipedal: How do Theories of Bipedalization Stand Up to Anatomical Scrutiny? In Anapol, F.C., Jablonski, N.G., German, R.Z. (Eds) *Shaping Primate Evolution*. Cambridge: Cambridge.
- Jolly, C.J. (1970). The Seed-Eaters: A New Model of Hominoid Differentiation Based on a Baboon Analogy. *Man*, 5: 5-26.
- Keith, A. (1923). Man's Posture: It's Evolution and Disorders. *British Medical Journal*, 1(3251): 669-672.
- Kingdon, J. (2003). *Lowly Origins*. Woodstock: Princeton University Press.
- Kortland, A. (1980). How Might Early Hominids Have Defended Themselves Against Large Predators and Food Competitors? *Journal of Human Evolution*, 9: 79-112.
- Kuliukas, A.V. (2002). Wading for Food: The Driving Force of the Evolution of Bipedalism? *Nutrition and Health*, 16: 267-289.
- Kuliukas, A.V., Milne, N., & Fournier, P.A. (2009). The Relative Cost of Bent-Hip Bent-Knee Walking is Reduced in Water. *Homo*, 60: 479-488.
- Kuliukas, A.V. (2011a). A Wading Component in the Origin of Hominin Bipedalism. In: (Verhaegen, M., Kuliukas, A.V., Vanechoutte, M., Eds) *Was Man More Aquatic In The Past? Fifty Years After Alister Hardy: Waterside Hypothesis Of Human Evolution*. Basel: Bentham.
- Kuliukas, A.V. (2011b). Langdon's Critique of the Aquatic Ape Hypothesis: It's Final Refutation, or Just Another Misunderstanding? In (Verhaegen, M., Kuliukas, A.V., Vanechoutte, M. (Eds) *Was Man More Aquatic In The Past? Fifty Years After Alister Hardy: Waterside Hypothesis of Human Evolution* Basel: Bentham.
- Langdon, J.H. (1997). Umbrella Hypotheses and Parsimony in Human Evolution: A Critique of the Aquatic Ape Hypothesis. *Journal of Human Evolution*, 33: 479-494.
- Lieberman, D.E., Bramble, D.R., Raichlen, D.A., Pontzer, H., & Cutright-Smith, E. (2006). The Human Gluteus Maximus and its Role in Running. *Journal of Experimental Biology*, 209: 2143-2155.
- Lieberman, D.E. (2007). Homing in on Early Homo. *Nature*, 449: 291-292.

- Lieberman, D.E. (2012). Those Feet in Ancient Times. *Nature*, 483: 550.
- Livingston, F.B. (1962). Reconstructing Man's Pliocene Pongid Ancestor. *American Anthropologist*, 64: 301-305.
- Lovejoy, C.O. (1981). The Origin of Man. *Science*, 211: 341-350.
- Lovejoy, C.O., Suwa, G., Spurlock, L., Asfaw, B., White, T.D. (2009). The Pelvis and Femur of *Ardipithecus ramidus*: The Emergence of Upright Walking. *Science*, 326: 71e1-71e6.
- Lovejoy, C.O., & McCollum, M.A. (2011). Spinopelvic Pathways to Bipedality: Why No Hominids Ever Relied on a Bent-Hip-Bent-Knee Gait. *Philosophical Transactions of the Royal Society London*, 365: 3289-3299.
- Marean, C.W., Bar-Matthews, M., Bernatchex, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Nilssen, P.J., Thompson, E., Watts, I., & Williams, H.M. (2007). Early Human Use of Marine Resources and Pigment in South Africa During the Middle Pleistocene. *Nature*, 449:905-909, (2007).
- Marzke, M.W. (1986). Tool Use and the Evolution of Hominid Hands and Bipedality (in Else, J.G. and Lee, P.C. (Eds.) *Proceedings of the 10<sup>th</sup> Congress of the International Primatology Society*, Volume 1. New York: Cambridge University Press, pp 202-209.
- McCollum, M.A., Roseman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O. (2010). The Vertebral Formula of the Last Common Ancestor of African Apes and Humans. *Journal of Experimental Biology*, 314B: 123-134.
- Merker, B. (1984). A Note on Hunting and Hominid Origins. *American Anthropologist*, 86(1): 112-114.
- Morgan, E. (1972). *The Descent of Woman*. London: Souvenir Press.
- Morgan, E. (1982). *The Aquatic Ape*. London: Souvenir Press.
- Morgan, E. (1990). *The Scars of Evolution*. Oxford: Oxford University Press.
- Morgan, E. (1997). *The Aquatic Ape Hypothesis*. London: Souvenir Press.
- Morgan, E. (2008). *The Naked Darwinist*. Eastbourne: Eildon Press.
- Morris, D. (1967). *The Naked Ape: A Zoologist's Study of the Human Animal*. New York: McGraw-Hill.
- Myers Thompson, J.A. (2002). Bonobos of the Lukuru Wildlife Research Project. In: (Boesch, C., Hohman, G., Marchant, L.F., Eds) *Behavioural Diversity in Chimpanzees and Bonobos*, Cambridge: Cambridge.
- Napier, J.R. (1964). The Evolution of Bipedal Walking in Hominids. *Archives of Biology*, 75: 673-708.
- Niemitz, C. (2002). A Theory on the Evolution of the Habitual Orthograde Human Bipedalism - The "Amphibische Generalistentheorie". *Anthropologischer Anzeiger*, 60: 3-66.
- Parker, S.T. (1987). A Sexual Selection Model for Hominid Evolution. *Human Evolution*, 2: 235-253.
- Potts, R.(1998). Environmental Hypotheses of Hominin Evolution. *Yearbook of Physical Anthropology*, 41: 93-136.
- Preuschoft, H., & Preuschoft, S. (1991). The Aquatic Ape Theory, Seen from Epistemological and Paleoanthropological Viewpoints. In Reynolds, V., Roede, M., Wind, J., & Patrick, J. (Eds) *Aquatic Ape: Fact of Fiction: Proceedings from the Valkenburg Conference*. London: Souvenir Press.
- Prost, J.H. (1980). Origin of Bipedalism. *American Journal of Physical Anthropology*, 52: 175-189.
- Ravey, M. (1978). Bipedalism: An Early Warning System for Miocene Hominoids. *Science*, 199: 372.
- Reynolds, E. (1931). *The Evolution of the Human Pelvis in Relation to the Mechanics of the Erect Posture (Rose)*. Cambridge: The Museum.
- Reynolds, T.R. (1985). Stresses on the Limbs of Quadrupedal Primates. *American Journal of Physical Anthropology*, 67: 351-362.
- Rodman, P.S., & McHenry, H. (1980). Bioenergetics and the Origin of Hominid Bipedalism. *American Journal of Physical Anthropology*, 52: 103-106.

- Roede, M., Wind, J., Patrick, J., & Reynolds V. (1991). *Aquatic Ape: Fact of Fiction: Proceedings from the Valkenburg Conference*. London: Souvenir Press.
- Rook, L., Moya-Sola, S., Kohler, M., Bondioli, L., & Macchiarelli, R. (1999). Oreopithecus Was a Bipedal Ape After All: Evidence From the Iliac Cancellous Architecture. *Proceedings of the National Academy of Sciences of USA*, 96: 8795-8799.
- Rose, M.D. (1984). A Hominine Hip Bone, KNM-ER 3228, from East Lake Turkana, Kenya. *American Journal of Physical Anthropology*, 63: 371-378.
- Rose, M.D. (1991). The Process of Bipedalization in Hominids. In: (Coppens, Y., & Senut, B., Eds) *Origine(s) de la Bipedalie Chez les Hominides*. Paris: CNRS.
- Sauer, C.O. (1962). Seashore - Primitive Home of Man? *Proceedings of the American Philosophical Society*, 106(1): 41-47.
- Sellars, W.I., Cain, G.M., & Crompton, R.H. (2005). Stride Lengths, Speed and Energy Costs in Walking of *Australopithecus afarensis*: Using Evolutionary Robotics to Predict Locomotion of Early Human Ancestors. *Journal of the Royal Society*, 2(5): 431-441.
- Shipman, P. (1986). Scavenging or Hunting in Early Hominids: Theoretical Framework and Tests. *American Anthropologist*, 88(1): 27-43.
- Sigmon, B.A. (1971). Bipedal Behaviour and the Emergence of Erect Posture in Man. *American Journal of Physical Anthropology*, 34: 55-58.
- Sinclair, A.R.E., Leakey, M.D., Norton-Griffiths, M. (1986). Migration and Hominid Bipedalism. *Nature*, 324: 307-308.
- Sokol, M.D., Raichlen, D.A., & Pontzer, H. (2007). Chimpanzee Locomotor Energetics and the Origin of Human Bipedalism. *Proceedings of the National Academy of Sciences of USA*, 104(30): 12265-12269.
- Stanford, C.B. (2003). *Upright - The Evolutionary Key to Becoming Human*. Boston: Houghton Mifflin Company.
- Stern, Jr., J.T. (2000). Climbing to the Top: A Personal Memoir of Australopithecus Afarensis. *Evolutionary Anthropology*, 9: 113-131.
- Sylvester, A.D. (2006). Locomotor Decoupling and the Origin of Hominin Bipedalism. *Journal of Theoretical Biology*, 242(3): 581-590.
- Szalay, F.S. (1975). Hunting-Scavenging Prothominids: A Model for Hominid Origins. *Man*, 10(3): 420-429.
- Tanner, N.M. (1981). *On Becoming Human*. Cambridge: Cambridge University Press.
- Thorpe, S.K.S., Holder, R.L., & Crompton, R.H. (2007). Origin of Human Bipedalism as an Adaptation for Locomotion on Flexible Branches. *Science*, 316: 1328-1332.
- Tobias, P.V. (1998). *The Aquatic Ape*: BBC Documentary.
- Tuttle, R.H. (1975). *Primate Morphology and Evolution*. The Hague: Mouton Publishers.
- Tuttle, R.H. (1981). Review of Lucy, By D Johanson: Paleanthropology Without Inhibitions. *Science*, 212: 798.
- Verhaegen, M., Puech, P-F., & Munro, S. (2002). Aquarboreal Ancestors? *Trends in Ecology and Evolution*, 17: 212-217.
- Verhaegen, M., Munro, S., Puech, P-F., & Vaneechoutte, M. (2011). Early Hominoids: Orthograde Aquarboreals in Flooded Forests? In Verhaegen M., Kuliukas A. V., Vaneechoutte M. (Eds) *Was Man More Aquatic In The Past? Fifty Years After Alister Hardy: Waterside Hypothesis Of Human Evolution*. Basel: Bentham.
- Walter, M. (2004). Defence of Bipedalism. *Human Evolution*, 19(1): 19-44.
- Washburn, S.L. (1960). Tools and Human Evolution. *Scientific American*, 203: 63-75.

- Wescott, R.W. (1967). Hominid Uprightness and Primate Display. *American Anthropologist*, 69: 738.
- Wheeler, P.E. (1984). The Evolution of Bipedality and Loss of Functional Body Hair in Hominoids. *Journal of Human Evolution*, 13: 91-98.
- Wrangham, R. (1980). Bipedal Locomotion as a Feeding Adaptation in Gelada Baboons, and its Implications for Hominid Bipedality. *Journal of Human Evolution*, 9: 329-331.
- Wrangham, R., Cheney, D.L., Seyfarth, R., & Sarmiento, E.E. (2009). Shallow-Water Habitats as Sources of Fall-back Foods for Hominins. *American Journal of Physical Anthropology*, 140: 630-642.
- Wynn, J.G., Alemseged, Z., Bobe, R., Geraads, D., Reed, D., & Roman, D.C. (2006). Geological and Palaeontological Context of a Pliocene Juvenile Hominin at Dikika, Ethiopia. *Nature*, 443: 332-336.